

EVOLUTION.—*The course of evolution.*¹ ROBERT F. GRIGGS,
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To evince an interest in orthogenesis or even to recognize that it is entitled to serious consideration by a scientific society is perhaps a somewhat dangerous admission. For many biologists consider orthogenesis a relic of the mystical childhood of evolutionary doctrine quite of a piece with the transmission of acquired characters and scarcely to be mentioned in a respectable Society. One authority expresses the feeling of many when he bluntly calls orthogenesis an "anachronism." Altenburg holds that "The theory of orthogenesis depends for its acceptance not so much on our knowledge of certain facts as it does on our ignorance of them."²

Yet the officers of the Paleontological Society ask me to open a discussion of the subject; because, in the words of their invitation, "The consideration of orthogenesis by the Society several years ago did not clarify the subject."

This statement again is an admission, at least that the subject is difficult to clarify. What chance is there of reaching a clearer understanding this time than on the previous occasion?

IS ORTHOGENESIS ESSENTIALLY MYSTICAL?

The zoologists' objections to orthogenesis so cogently set forth during the earlier discussion by Dr. Friedmann boil down, I believe, to the supposition that orthogenesis is essentially a mystical interpretation of evolution which calls into play not only unknown but unknowable agencies which are beyond the reach of scientific inquiry, that orthogenesis is really a Doctrine of Faith rather than a Law of Science. In so far as this is correct, the subject is certainly out of reach of scientific discussion; and if this be the whole truth, we can no more hope to reach a decision on orthogenesis than we could on one of the questions debated by the old Scholastics.

But if orthogenesis were, wholly outside the realm of evidence, it would in these modern days no longer constitute any problem at all. Its difficulty lies exactly in the fact that both natural and supernatural considerations have entered into its discussion. The problem is then to disentangle these elements. Needless to say, I shall not attempt to consider the mystical elements—not because I disbelieve in a theistic universe but because as I have said, that is a matter for

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² ALTENBURG, EDGAR. *How we inherit*. P. 120. 1928.

faith and is not susceptible of proof or disproof by scientific methods.

As in any controverted subject, we may well begin with a definition. Is it correct to state that the essential feature of orthogenesis is that it holds that evolution proceeds in definite directions rather than at random—that the course of evolution follows definite trends? And further it is usually held, I believe, that the tendency to fall into such definite lines of evolution is characteristic of the nature of protoplasm itself. Other elements which have entered into the conception are, I think, mostly concerned with external causes of the trends and are, in the absence of any real understanding of such causes, mystical, or, to say the least, highly speculative.

Observers are not wanting, however, who strike at the very idea of evolutionary trends quite apart from any considerations as to cause. Altenburg says flatly that orthogenesis "contradicts all that we know about mutations, especially as shown by the careful studies made on the insect *Drosophila*," and again, "The mutation theory also makes untenable the theory of orthogenesis, according to which changes take place along predetermined lines and not in all directions as demanded by the mutation theory."

Here we have clearly set down the divergence in philosophy that has arrayed biologists in two hostile camps, the one dominated by the zoologists and the other by the paleontologists.

Is evolution haphazard, produced by mutations which occur in a miraculous manner, essentially supernatural in that they are caused by circumstances entirely outside of the ordinary run of nature? In this view, the only means by which the orderly relationships which we observe throughout nature could be produced is by natural selection. The adherents of such a theory account for the steady progress of the Equidae from a primitive five-toed ancestry down to the single-hoofed horses of today by the natural selection of random mutations alone. This theory would seem to me to put its adherents under a serious disadvantage at the start by imposing on them the necessity of proving that at every step in the evolution of the horse each slight decrease in the size of the lateral toes was an advantage great enough to favor in the struggle for existence those individuals which possessed it over those which did not.

Not all the geneticists, even though they have no use for orthogenesis, adopt this extreme view. Newman³ states a very much stronger and I believe more generally held position when he writes, "It should be said that definitely directed evolution is now believed

³ NEWMAN, H. N. *Readings in Evolution*. 3rd ed., p. 36.

to be one of the laws of organic evolution but we have no clear ideas as yet as to what are its underlying causes. Therefore *orthogenesis is not a causo-mechanical theory of evolution at all.*" (Italics in original.) Having thus delivered themselves, the geneticists smugly withdraw to their milk bottles to nurse their *Drosophila* and the paleontologists may throw as many of their figured stones at them as they please without in the least disturbing their self-satisfied self-sufficiency.

If the attitude of the unorthogenetic brethren were entirely snobbery, it would not last long and we would not need to concern ourselves with it. The truth is, however, that they have opened up a serious weakness in the orthogenetic position. In the minds of many men, the theory of orthogenesis shares with the so-called theory of special creation the onus of being merely a pseudo-explanation of the facts with which it deals. They hold that it substitutes a name for an explanation and really carries its adherents not one step closer to an understanding of the facts. Worse than that, they feel that instead of clarifying and stimulating thought, it puts it to sleep.

In so far as this has been true, orthogenesis deserves all the contempt with which it is held in some quarters. Certainly the paleontologists want to be very careful to purge themselves of every vestige of this sort of loose thinking before they take up the cudgels in its defence.

But on the other side, are the geneticists, having admitted the reality of orthogenesis, justified in dismissing it from further consideration because we do not understand its causes? If this is a proper attitude we should also drop all consideration of evolution itself for assuredly we know very little about its causes either.

If we agree that we have no comprehension of the causal factors at work there yet remains the very large task of mapping the evolutionary trends which are observed. And since some disbelieve in the very existence of orthogenetic trends, it may be advisable to reassemble the evidence which appears so convincing to the adherents of the theory. Yet it would seem that the old masters like Cope have done that well enough and that it would be better to refer to the literature. In any case, I shall not undertake this task but will concern myself merely with another side of the question. True or not, is the study of orthogenesis worth while?

It is an axiom that the value of a scientific theory depends not so much on its truth as upon its usefulness. The reason lies of course partly in the difficulty of ascertaining absolute truth and partly in that our problem is to master our environment. The question really

before us is then, I believe, not is orthogenesis true but is it of any good to us? Can we make orthogenesis bring forth useful results?

It is to that question then that after this preliminary clearing of the ground I would address myself.

Very definitely I believe that due consideration of the conclusions which orthogenesis demands would greatly strengthen taxonomy if indeed it did not give us a whole new outlook upon the plant and animal kingdoms. For I believe it can be demonstrated not only that evolution proceeded orthogenetically but that the orthogenetic lines in many groups of organisms, both animals and plants, have pursued similar trends, in other words that evolution runs a definite course and that the course has followed the same paths in entirely unrelated phyla.

For that reason I have entitled my discussion *The course of evolution*.

I. AGGREGATION AND MULTIPLICATION

The first stage in evolution, after the living units themselves have been produced, is aggregation or multiplication. This occurs at many levels all along the line from the lowest to the highest. (1) Dividing cells, failing to separate, form colonies and multicellular animals. (2) In the fern-allies, the sporophylls become aggregated into cones which are the starting point for all the complex evolution of the flower. (3) In the lower invertebrates, segmentation into a series of similar somites, as in the annelid, lays the foundation for most of the evolution of the animal body.

(4) In corals and jellyfishes, where asexual reproduction by budding plays a large role, the daughters often fail to separate and make possible complex polyzoid individuals closely resembling the colonial vorticellas except that the bells are multicellular individuals instead of single cells.

(5) The single meristems of lower ferns and cycads multiply in higher types until a freely branching plant body is produced. Exactly similar branching bodies with many terminal branches are produced in a number of unrelated groups of sedentary animals such as ascidians, sponges, bryozoans, and in at least one crustacean, *Thompsonia*.

(6) In the highest flowering plants the flowers, originally solitary, become aggregated into clusters with reduction of the subtending leaves to bracts and the clusters take on an individuality of their own, and become the well-known composite heads of the aster family.

Here special leaves simulate sepals, special flowers, petals, etc. This achieved, the composite clusters start out on an independent evolution of their own, repeating many of the steps earlier taken in the evolution of the solitary flower.

(7) Again in the grass family, we find the individual flowers, reduced to their lowest terms, associated first in loose panicles, then brought close together until, in all but the very lowest bamboos, the aggregate becomes a new unit, the spikelet, which again goes through a complete cycle of evolution on its own level. (8) Then clusters of spikelets go through another parallel cycle of evolution on a higher level, until finally such a complex unit as the ear of maize appears on a still higher level.

In short, wherever you find organisms or organs tied together in permanent association, you may expect to find the development of a new unity and the beginning of a new cycle of evolution.

(9) Even where the units are not stationary, something of the same nature occurs as, for example, in the social insects where assuredly the organic unit is the colony like the hive of bees and not an individual such as the worker. The queen bee has become essentially only an organ of the colony—its ovary. True, she retains her eyes, legs, wings, and other organs but so, in the multicellular body, does every cell retain the fundamental structures and functions of the original free-living protozoon.

I need hardly add in these troublous times that most of the problems of human society spring from the fact that we have not yet learned how to associate in larger units and that, if we do not exterminate ourselves in the process, evolution will surely carry us into some form of collective unity. Already this industrial age has made impossible any such individual independence as that of our pioneer grandfathers who settled this continent in isolated self-sufficient groups.

In studying the evolution of any one of these aggregates, we see that in some way living units in close proximity inevitably influence each other's development, and here we approach an understanding of the cause of orthogenesis. We may return to seek explanatinos later, but now we must go on with the process itself.

As has appeared from the mere catalog of various types of aggregates, aggregation is the foundation on which later evolutionary processes are built. Once the aggregate—colony, tree, flower cluster, or society—has been established, evolution follows a rather definite course.

II. REDUCTION

A. *Reduction in number of similar parts*

The next stage after the preliminary aggregation has been completed is a reduction in the number of similar parts.

Flower parts.—The lowest flowers, both monocot and dicot, like magnolias, buttercups, sagittarias, anonas, potentillas, and water-lilies, have large numbers of flower parts: 50–100 sepals, petals, stamens, and/or carpels as the case may be. That these are really the most primitive of the flowering plants is evidenced by the fact that in these types, and in no others, monocots and dicots come close together. The flowers of the dicot buttercup and the monocot *sagittaria* are practically indistinguishable. All of the higher types have the parts reduced to smaller numbers: 6-5-4-3. In many cases there are vestiges of the larger numbers formerly present.

There is, further, good evidence that various types of both dicots and monocots have radiated from a common type similar to the polymorous buttercups and *Sagittarias*.

Gill arches.—A similar reduction in the number of gill arches occurs in the lowest chordates. *Amphioxus* has 100 or more. In the cyclostomes, *Bdellostoma* has 15 to 10, other cyclostomes 9 or 8. In the elasmobranch sharks, *Heptanchus* has 9, *Chamaeselachus* 8, but the usual number is 7; while in ordinary fishes it is reduced from 6 in the embryo to 4 in the adult, but some fishes have lost one or two of these, leaving 3 or 2.

Segments.—In a general way, the phylogenetic order of several classes of invertebrates corresponds with the number of their somites. Annelids have more segments than millepedes and, of course, are far more primitive. Millepedes have more than centipedes; centipedes more than scorpions; scorpions more than insects.

Among crustaceans, branchiopods like *Apus*, with forty to sixty-three pairs of trunk limbs, are nearer the aboriginal type than *Malacostraca* like the crayfish with fourteen trunk appendages, and they in turn are more primitive than hermit crabs and true crabs which have lost or nearly lost their abdominal appendages.

Vertebrae.—The lamprey may have 400 vertebrae. Among the elasmobranchs, *Alopias* may have more than 200 in the tail alone, *Raja* about 150, while *Heptanchus* has only a few more than 100. The cod has 52, man 33.

Teeth.—The sharks have several hundred teeth. Teeth are still very numerous in the teleosts and may be present on all the bones of

the mouth. In the Amphibia, there is in general a considerable diminution in the number of teeth as compared with the fishes, but they still occur regularly on vomer and palatine in addition to maxilla and premaxilla and sometimes develop on the parasphenoid as well.

In reptiles the teeth are still numerous and widely distributed on several oral bones.

Up to the mammals, there is generally an indefinite succession of teeth throughout life, so that any loss is promptly replaced. The European viper, for instance, has as many as nine poison fangs in reserve which come into play successively as their predecessors may be torn out.

In the mammals, succession is reduced to the familiar two sets of teeth, and there is a plain tendency both further to reduce the number and do away with the division into two sets. The opossum has fifty teeth, but the ideal placental would have only forty-eight, and on account of losses here or there none exceeds forty-four except some of the whales whose teeth constitute a special problem. To be more

specific, the dental formula of the dog is $\frac{3-1-4-2}{3-1-4-3} = 42$, but in the cat

the teeth are reduced to $\frac{3-1-3-1}{3-1-2-1} = 30$. The lynx is made a separate ge-

nus because it has lost the first premolar of the upper jaw, and brought

the dentition down to $\frac{3-1-2-1}{3-1-2-1} = 28$.

The losses of specific teeth among the mammals, however, are obviously of a different character from the general reduction in number met in the lower classes and bring us to the consideration of the next type of orthogenetic trend.

Before going on, however, a caution should be noted.

Nobody should suppose that in any of these cases, we are attempting to cite actual lines of descent. The evidence indicates, rather, and I think most students would agree, that the actual ancestors of the higher forms listed passed through stages where the organs in question (not necessarily the whole organisms) corresponded with the earlier stages given.

Nor could it be maintained that recognition of the sequence in such cases as have been given could be of much use to taxonomy. In most of these cases everybody recognizes the more primitive types

from other criteria. Useful applications of this and the other principles to be given are to be had in working out the status of smaller groups which are made up of species much more closely related. For illustrations of this sort, I must turn back to the plants which I know better.

Take the tribe of grasses known as Festuceae. In *Eragrostis major*, there are 40 to 10 similar flowers; in *Eragrostis minor*, 20 to 8; in the related blue grass, *Poa pratensis*, 5 to 3. In *Cynosurus*, the fertile spikelets are 3- to 2-flowered. *Lamarckia* has numerous vestigial flowers in the sterile spikelet, and in the fertile, one perfect flower with vestiges of a second.

In the Chlorideae, *Leptochloa* has 12 to 3 flowers; Eleusine 7 to 3; *Gymnopogon* rarely 3 or 2 but normally only 1; *Bouteloa* several flowers, all but one vestigial; and *Cynodon* is constantly one-flowered.

In the Hordeae, *Agropyron Smithii* has 13 to 7 flowers; *Agropyron repens* about 5, *Agropyron pauciflorum* 2, barley and all the highest most specialized genera are reduced to one flower.

In the higher tribes of grasses, the spikelets are uniformly one-flowered, but vestiges of a second flower are usually present. These are, however, in different relations to the fertile flower, thus indicating independent but parallel reduction from different ancestors.

B. Fixation in the number of parts

The third of the orthogenetic trends I shall mention is inextricably associated with the preceding. Not only are the numbers of parts reduced but the number is fixed. In the earliest stages, the numbers are large and indefinite. They become smaller and definite.

Not only do mammals have less teeth than the lower groups, but the number of teeth is nearly always constant, and even varies comparatively little even in the large groups. Not only are the petals of ordinary flowers reduced to 6-5-4 or 3; they are, with only minor aberrations, fixed at 6 or 5 or 4 or 3, and as all of you know, these numbers are characteristic of whole families or even orders.

The same trend occurs in the higher level of the flower cluster of the aster family. In most composites, the number of disc flowers, ray flowers, and bracts is large and indefinite; but here and there the head has been reduced to a definite organization. Thus, in *Cosmos* and related genera, there are 16 bracts in the involucre in two sets of 8 each and 8 ray flowers, each set alternating in position with the one outside it. In our common *Chrysogonum*, the involucre is made up of 10 bracts in two sets of 5 each, the inner of which wrap around the

ovaries of the 5 fertile flowers. Other flowers are present but vestigial.

So on down the list in each of the illustrations cited above and throughout nature generally, the numbers of parts become fixed and standardized at a relatively early stage in evolution; and thereafter the reductions which occur are, like the loss of the vestigial premolars in the lynx, very minor compared with the wholesale reduction that occurs earlier.

C. Consolidation

At a third stage in the reduction process, other tendencies begin to creep in which later become manifest in the development of new units. Primitive types are loosely knit. During the course of evolution they become more and more compact.

In plants, consolidation expresses itself especially in the organization of flowers and flower clusters. Primitive flowers were solitary. Next they began to aggregate into loose clusters, the stems of these shortened produce simple *racemes*; further shortening of branches gives rise to unbranched *spikes*; the main axis then shortened, drawing all the flowers down into a compact *head*.

Similarly the axis of the individual flower is shortened from the primitive condition of a pine cone seen in *Magnolia* to the stage of most flowers where the parts, instead of spiralling up an elongated axis as in the cone, are in circles one above another.

Although this completely-eliminated axis might seem to represent the theoretical limit, stoppage of axial elongation goes much further in many families where the axial growth is inhibited before lateral growth is complete, with the result that the lower parts pile up around the center and the flower turns itself inside out, so to speak. Thus, an epigynous flower is produced in which the parts originally basal—sepals, petals, and stamens—are carried up around the ovary. In some cases, as in four-o'clocks, roses, and lythrums, the tube grown up around the ovary remains free from it but in a large majority of such flowers, the elevated parts grow fast to the ovary as in apples, melons, blueberries, and gooseberries.

This orthogenetic trend is so characteristic and prevalent that it appears independently in many unrelated orders. To those mentioned we might add honeysuckles, composites, lobelias, cacti, begonias, aralias, carrots, and hydrangeas.

The mouth parts of arthropods, originally the segmental appendages of the somites in the oral region are in all but the lowest forms brought into close contact and fitted together around the mouth. As

in the flower clusters there is remarkably little tendency toward fusion of the separate appendages.

Our own skull is as notable an example of this sort of thing as any. The skull of primitive vertebrates consisted of a loose basket-like aggregation of separate bones in which the mandibular, the auditory, the ocular, and even the olfactory regions were distinct units hung around the cranium but by no means a part of it. Here again although complete unity has been achieved by closely interlocking sutures, there is remarkably little fusion of bones.

The same tendency toward consolidation of loosely arranged structures is manifest in the nervous system of arthropods. The primitive groups have a double chain of ganglia strung along the length of the body. But the commissures between these have shortened up in all higher forms. Here, as in the development of inferior ovaries in flowers, the consolidation of the parts carries us much further, into another type of reduction which is the next step.

D. *Coalescence of free parts*

The fusion of parts originally separate is carried out even more conspicuously in flowers by horizontal fusions than by the vertical concrescence around the ovary described in the development of flowers with inferior ovaries.

The recognized distinction between lower and higher dicots is in the fusion of the separate petals, such as we find in pansies, into united corollas, as in petunias. Traces of the originally separate petals remain as ribs of the united corolla as in morning-glories or as projecting lobes as in phloxes. While all of the highest dicots thus have sympetalous corollas, there is abundant evidence that fusion really occurred and/or perhaps is still occurring over and over again independently in scores of families, as for instance in the Leguminosae where the flowers are certainly polypetalous but show varying degrees of fusion in many different genera. In the heath family, Labrador tea has separate petals but in most of the genera they are fused as in Azalia and Mountain laurel. In the olive family, the petals of fringe-tree and forsythia have barely united at the base, but those of lilac are joined half-way up.

All the other flower parts show the same tendency, and there is every evidence that fusion has occurred independently in many unrelated families. Thus we have united sepals in the calyx of a carnation, united carpels in innumerable fruits like orange, apple, banana, melons, etc. etc.

The trend toward fusion frequently reappears in clusters of flowers. Thus, a mulberry (*Morus*) resembles a blackberry, but while the blackberry is produced by the partial coalescence of the carpels of one flower, the mulberry is due to the fusion of many flowers, each one of which becomes a lobe of the fruit; and this tendency, manifested in various ways, is characteristic of the whole family Moraceae, e.g., bread-fruit and fig.

A pineapple is a similar aggregate. The fruit which we eat includes the bracts as well as the ovaries of the many flowers as can be readily demonstrated by inspection of the fruit or more clearly yet, of the numerous showy blossoms at flowering time.

Fusion of parts originally free is equally marked in animal organs. Everyone who eats chicken notes that the backbone in which the vertebrae, which may still be readily counted, is united into two units, one supporting the wings and the other the legs. That this consolidation has developed in the class Aves is shown by a glance at *Archaeopteryx* where there is little more fusion of vertebrae than in reptiles.

The segments of the originally simple arthropod body have been consolidated, as everybody knows, into the most highly differentiated cephalothoracic regions of insects, crustaceans, and spiders until decision as to the exact number of segments of the aboriginal ancestor has become as difficult as in the vertebrate skull.

The brain of arthropods and apparently that of vertebrates also originated in similar fashion.

E. *Elimination of some organs*

After large and indefinite series of organs have been reduced to small and definite numbers, the next step in the reduction process is the complete elimination of some sets.

Among flowers, the loss of petals or sepals or stamens or carpels is exceedingly common. Very often elimination has not been quite complete and tell-tale vestiges of the lost organs remain.

Elimination of floral organs has occurred, so to speak, both wholesale and retail. There are whole regions of the Angiosperms where the flowers have been reduced almost to their lowest terms such as the grasses, sedges, willows, hickories, oaks, birches, and spurge. Many individual genera or even single species in families with complete flowers have also suffered similar losses, as for example *Isnardia* in Onagraceae, *Aruncus* in Rosaceae, some species of ash in Oleaceae.

Great confusion has resulted among botanists from failure to

understand that these flowers are reductions. It used to be supposed that such rudimentary flowers as willows and poplars were primitive and that evolution had proceeded by the addition and division of parts until finally the complete polymeric flowers of buttercups were achieved. There is no occasion here to go into the merits of this old controversy. Suffice it to say that if the terminal reduced twigs of the phylogenetic tree are regarded as relics of former main trunks, it is as difficult to find the connections with the roots as it would be if a similar attempt were made with an oak tree. Worse yet, each separate twig would require a different root and the family tree would become polyphyletic with a vengeance!

One of the most fundamental eliminations of organs is in the sex organs of the vertebrate. The male and female sexes start development alike, clearly pointing back to a primitive hermaphroditic condition. The embryo lays down two urinogenital outlets on each side, the Wolffian and the Muellerian ducts. In the male, the Wolffian duct becomes the seminal duct and the Muellerian atrophies. In the female, the Muellerian duct becomes the Fallopian tube and the Wolffian atrophies.

Eliminations in animals are so numerous and generally recognized that there is hardly need to point them out. Snakes have lost all their limbs, and some boas retain vestiges to prove it. Whales and sea cows have lost their hind limbs. *Dinornis* has only the slightest vestiges to show that it ever had wings, and other flightless birds like cassowaries, apteryx, and the ostriches show various stages in the loss of their wings.

III. DIFFERENTIATION

A. *Differentiation of parts originally similar*

Soon after the number of parts is fixed, differentiation sets in. Parts originally similar become specialized to subservise diverse functions. Similar spike teeth segregate into incisors, canines, and molars. The vertebrae, all alike in the fishes, diversify until each one takes on peculiarities of its own.

In flowers, the regular radiate blossom with petals all alike becomes a very irregular lipped flower like an orchid, a pea, or a snapdragon. All stages of the process may be seen in many unrelated families. The lowest member of the figwort family is the familiar mullein with almost regular flowers still retaining the primitive 5 stamens. From this there is a complete series to the most irregular flowers like snapdragons and louseworts in which the stamens are reduced to 4 or 2

and twisted out of all semblance to the straight and regular organs of the ancestral flower.

In the Leguminosae, all transitions from regular flowers like *Mimosa* through *Cassia* down to the highly one-sided peas are familiar.

No such series occurs in the orchids, all members of the family having very highly one-sided flowers, but botanists place orchids at the summit of the monocots for exactly this reason. That is, though the stages in their differentiation are gone, we recognize the applicability of the rule in assigning them this position.

B. *Progressive sterilization*

The original and most fundamental differentiation was the sterilization of most of the cells in the body. In the original unicellular organisms all cells were of course reproductive. The most primitive colonies are in the same condition. But very early reproductive functions were restricted to special cells. From that time on, a large part of the course of evolution has centered around a continuously progressive sterilization of reproductive tissues with accompanying differentiation of the sterilized elements into vegetative organs.

This is hardly the place to call attention to the fact that the so-called "race suicide" of the cultured classes, which bothers us so much, is a homologous biological phenomenon. How serious it may become we cannot guess, but we may remark that there was probably no occasion to worry over the "suicide" of the first brain cells.

But this aspect of progressive sterilization, followed by differentiation, brings us to another well-known characteristic of living organisms.

IV. SUBSTITUTION OF ONE FUNCTION FOR ANOTHER

All of you are familiar with the fact that almost every new organ of animals and plants consists of an old one made over to serve a new function.

Stamens and carpels are clearly "made-over" leaves. This is not manifest from inspection but is clearly demonstrable by study of comparative anatomy.

Similarly, petals and sepals are as definitely sterilized stamens made over into new functions. While the original differentiation of sepals and petals occurred in the unknown ancestry of the Angiosperms, the orthogenetic tendency in that direction continues in many families.

The flower of canna has its full complement of both sepals and

petals, but those are not what you see when you look at a canna flower. The conspicuous part of this flower consists of sterilized stamens enlarged and made petaloid. Only one-half of one stamen remains functional, riding like an appendage apparently out of place on the big staminode to which the rest of it has been transformed.

The tendency to make stamens over into petaloid structures is pronounced throughout the higher monocot families, viz., in bananas, gingers, arrowroots, and orchids as well as in cannas.

But the same tendency is latent in many families of flowering plants, dicots as well as monocots, even though it does not normally come to expression. Many of the "double" varieties, which occur in almost all types of ornamental plants, are produced simply by the conversion of stamens into petals, as you may see by comparing wild roses with our hybrid tea types.

The metamorphoses of fins of fish to legs, of the forelegs to flippers in whale, to wings in bats and birds, are too familiar to be mentioned. The scales on the top of the fish's head became part of the bony skull.

It is so obvious that there is no need of saying it that a species with metamorphosed structure has been derived from one unchanged. The point for us here is that such metamorphoses take a long time, that there are many stages in the process which therefore constitutes an orthogenetic trend.

V. ANNEXATION OF ACCESSORY PARTS

The tendency toward consolidation often goes far beyond the organs immediately concerned. It seems as though a definite principle of organization grips all living structures which come close enough together to establish interrelations.

Many familiar examples will occur to you. The scales of the winter bud which protect the head of dogwood flowers expand at flowering time into the large white petaloid structures which make the dogwood so beautiful. The topmost leaves of the poinsettia take on the bright red which makes them desirable for Christmas decorations. The leaves below the head in the composites are brought into the organization and become analogous to sepals. The bracts subtending the flowers of grasses, becoming glumes, carry on the subsequent evolution of the group. In some grasses, where the spikelets are brought down close to bracts of a second order, these in turn are taken into the organization and become functionally comparable to glumes, as in the husk of maize or the hull of a sand burr.

Again when in composites the heads with their bracts are brought

close together in the axils of lower leaves, these may become to all intents and purposes involucral bracts, and the compound head starts on a new line of evolution as in our common *Elephantopus* where the marginal ray flowers radiate, not from each head, but from the center of the cluster of heads, making the cluster analogous to a single flower.

In the pineapple, pulpefaction spreads from the ovaries through the bracts, and in some tropical varieties when fully ripened, to the main axis of the flower cluster as well.

The fact that our unified vertebrate head was achieved by the addition of gill arches and other organs originally separate entities has already been alluded to.

VI. THE NARROWING POSSIBILITIES OF EVOLUTION

As the evolution in any group proceeds the possibilities of diversification continually contract.

In the beginning, unrestrained by heredity, variations had free rein. The differences among unicellular organisms are more fundamental than those between the most diverse of the higher organisms. Blue-green algae, diatoms, ciliates, rhizopods, slime molds, and bacteria differ far more among themselves than do higher plants from higher animals. Among the bacteria, for instance, we have one group which has built its metabolism around the oxidation of sulfur, and another which oxidizes iron as a source of energy, while the protoplasm of all higher organisms is built on carbon chemistry.

The cytology, nuclear behavior, and consequently the heredity of all higher organisms, both plants and animals, is essentially the same. Otherwise, Mendel's law could not hold in guinea-pigs as in peas. But among unicellulars there are several entirely different types of cell organization the mechanism of which would preclude Mendelian inheritance.

Like most other laws of evolution, this narrowing path of progress finds a perfect analogy in human artifacts. Take the automobile. Those of you who can remember the early days of "horseless carriages" will recall the fundamental diversity of the early types. Beside gas buggies, there were steam and electric carriages. They were high-wheeled and low-wheeled with cushion tires, as well as pneumatic. Among the gas engines, some had one cylinder, some two, as well as others with four. A fundamentally different type of transmission survived for many years in the old Model-T Ford.

The history of the automobile gives a clear answer to the cause of

the phenomenon. The diverse early types were eliminated by what amounts to natural selection. As the better types were proven out in use, it became impossible to sell the others until today all cars have approached so closely to a common standard of excellence that there is little to choose among them and the manufacturers fearing to adopt radical departures such as putting the motor in the rear have begun to waste their energies on inconsequential gadgets.

This is exactly the situation among organisms. In the early stages, protoplasm can go off into all sorts of experiments but as the type becomes fixed, heredity restricts variations to minor features and in the end we get mere diversity without any real difference. Many authors have called these later stages "speciation" and have emphasized the differences between speciation, evolution with a small *e* and Evolution of the larger characters, Evolution with a big *E*.

Dollo's well-known "law of the irreversibility of Evolution" is, of course, only a special case of the broader law of the narrowing possibility of variation.

Only two examples of the fundamental diversification which occurs in primitive groups may be given. Among primitive Notoungulata, a fossil order of hoofed mammals peculiar to South America, Simpson⁴ found in the animals in a single quarry, i.e., those living together as one species in one time and at one place, characters upon which had been based seventeen species, seven genera, and three families.

The important consideration for us is: the criteria by which these families, genera, and species had been founded constitute valid distinctions for separating such groups among the later, more advanced members of this same order.

Among plants, the primitive family Anonaceae has more different kinds of floral structures than are to be found in any other one family, some of them not duplicated anywhere else among flowering plants. Yet indubitably all are closely related and properly placed in a single family.

This narrowing of the path of evolution seems to me to refute the claim of the geneticists that mutations are purely at random. You might as well argue about the random aberrations of a canal boat swinging on its tow-rope as compared with the course of a ship on the open sea, as to conclude that the random mutations of *Drosophila* tell us much about the evolution of insects.

I am not trying to minimize the importance of the mutations of *Drosophila*. They have been the key to wonderful advances in our

⁴ SIMPSON, G. G. *Supra-specific variation*. Am. Nat. 71: 247. 1937.

understanding of inheritance. But their relation to the evolution of insects has yet to be made known.

Those inclined to believe that changes significant for evolution occur at random would do well to ponder the implications of a paper by one of the greatest of geneticists, N. I. Vavilof, entitled, *Homologous variation*.⁵ Assembling all the species and varieties of cultivated plants and their relatives in his experimental gardens, Vavilof observed that related types repeat over and over again the same series of characters, i. e., that homologous mutations had occurred in related types.

For instance, there are three groups of wheats. In the first group, *Triticum compactum* and *T. spelta* are closely allied to *T. vulgare* and repeat all the varieties of it.

The second group repeats the varieties of the first, e. g., there are varieties with white, red, and black ears; smooth and hairy ears; with white and red grains; winter and spring wheats; only beardless varieties are unknown.

The third group repeats the varieties of the second.

The similarity of the characters of the varieties of the three species of pumpkins, *Cucurbita maxima*, *C. pepo* and *C. moschata* interested Darwin who thought it accidental. Vavilof brings it under the reign of his law of Homologous variation. He shows further that the species of related genera show the same homology in their variation. Thus *Cucurbita* (pumpkin), *Cucumis* (cucumber), and *Citrullus* (watermelon), all have types with fruits round, oblong, flat and segmented; white, green, yellow, brown, black; monochrome, streaked, or spotted; each has both sweet and bitter varieties; and all show homologous variations in color and hairiness of petals.

He lists 34 homologous variations that have occurred in both wheat (*Triticum*) and Rye (*Secale*) and shows that the related genera *Agropyrum* and *Aegilops* though studied in less detail repeat in general the same series.

Following up his belief in homologous variation Vavilof sent out expeditions to search for varieties with characters known only in related types and was successful in finding them, very much as the chemists have filled the gaps in the periodic table of the elements.

The very homology in the mutations responsible for these characters by itself disposes of any supposition that they occurred at random. The same force must have acted independently in each of these parallel mutations.

⁵ Journ. Genetics 12: 47-89. 1922.

While much of the convergence observed in plants and animals is clearly adaptive like the streamlined bodies of fishes, whales, seals, and manatees, most of the homologous characters dealt with by Vavilof are of no conceivable use to the organism and furnish no handle for natural selection to take hold of.

If they were useful their adaptiveness would necessarily be alternative. That is, natural selection would have preserved the more useful, for example, say leaves without ligules, and eliminated the others, leaves with ligules.

APPLICATION OF ORTHOGENESIS TO RESEARCH

I have listed some of the orthogenetic trends characteristic of organisms, and I have given data enough, I think, to prove their reality. Certainly more could be supplied to the extent that time and space permitted. Our further task is to apply such information to the problems of taxonomy.

One illustration of the use of those considerations, which occurred right here in our midst, was Hitchcock's treatment of the grasses. When he wrote the Gramineae for Gray's *Manual* in 1908, he used the old conventional system which put maize at the beginning, but in his *Genera of grasses* 1920, he adopted a system in accord with the orthogenetic trends here listed.

The difference in the mind of a student is very much the same as the enlightenment which suddenly dawned on all biologists when they first looked at organisms from the point of view of evolution. Like the theory of evolution itself it gave meaning and coherence to a mass of heterogeneous detail which before had been merely a burden on the memory.

If it be granted that every group of plants should be set into such an orthogenetic order and that the same should be done for animals, it must be recognized that the accomplishment of such an undertaking is a task not only of large magnitude but of considerable difficulty as well.

It might seem that, given the guiding principles, any child could make the applications. But it is not so. Although these orthogenetic trends are general characteristics of organisms, they are not organismal.

Each trend pursues its own course independent of all the other trends to which the organism is subject. One genus may have gone far in reducing the numbers of its parts but have made no progress in differentiation or in the fusion of parts. Another genus in the same

family will show much differentiation but retain a primitive number of parts. That is, most close-knit groups of organisms can be arranged in various ways, depending on which of the orthogenetic trends present is used as the basis of classification. The problem of the taxonomist is to decide which of the trends present is most significant in the case in hand.

COMPETITION A POSSIBLE EXPLANATION OF ORTHOGENESIS

Before closing it will be well to take up the question of the cause of orthogenesis which I sidestepped at the beginning. I repeat that whether we understand it or not, orthogenesis must be accepted as the way of evolution. Yet we will never be satisfied until we penetrate the mystery and reveal the cause. It is unnecessary to say that I am not prepared to discuss this question with any degree of assurance or of specification, but there are some simple and well-known biological principles which may have a large bearing on the problem.

Why should there be a reduction in numbers of parts? Remembering that in the beginning of aggregation of cells—and to a considerable extent ever since—each individual cell maintains its own fundamental entity, we may ask why some should be eliminated. The answer comes to our lips almost automatically: It is the fittest, or more accurately, it is the most favorably placed, that survive.

In marvelling at coordination characteristic of multicellular plants and animals, we are apt to forget that their individual cells and organs are still in competition with each other. But we see examples of this fact every day in the buds of a tree which are laid down in numbers far beyond the possibilities of development. If some are removed, others which could never have developed in the presence of more favored competitors begin growth. It has been proven that the dormant buds are suppressed by the growth of the dominant ones. There is a metabolic gradient from the dominant leader backward and inhibiting hormones are sent back from the leader which prevent the growth of subordinate buds.

Similar metabolic gradients are characteristic of the animal body. They have been studied extensively by C. M. Child. He found that the orientation of the body is definitely controlled by these metabolic gradients. In simple planarians he was able experimentally to alter the metabolic gradients. By doing so, he was able to shift the head of the animal around almost at will.

No one has attempted to see how far metabolic gradients could be instrumental in directing the evolution of the race as they certainly

do determine the development of the individual. In view of the similarity of the two cases there is no more occasion for assigning mystical agencies as the cause of orthogenesis than there is for bringing them into the explanation of the development of the individual.

Again a geneticist would say that the variations reported by Vavilof are homologous because the genetic constitution of related types is homologous. Given the closely similar gene complexes, closely similar mutations would be expected. This again is, however, only a restatement of the Law of the narrowing possibility of evolution.

Finally, it should be pointed out that these orthogenetic trends are largely unadaptive. In a few cases, such as the differentiation of the teeth, advantages to the organism may be made out. But generally, nothing of the sort can be imagined. For the most part, the adaptive sequences in evolution are superposed on the great orthogenetic trends but are entirely independent of them.

In the spurge family, Euphorbiaceae, for example, there is an orthogenetic series in the reduction from fairly typical flowers down to vestiges which could never be recognized as flowers if we did not have a complete series of integrating transitional forms. But no one could pretend that this change is advantageous. Alongside this, and entirely unrelated to it, is a modification of the plant body from that with typical leafy shoots into a series of leafless desert plants so similar to the cacti that they can be told apart only by technical characters. The independence of orthogenesis from environmental stimuli has been pointed out by many writers and there is no time to elaborate or further to illustrate here.

Our concern with the lack of adaptiveness in the main trends of evolution is its relation to the claims of the geneticists. In their belief, the orderliness of nature has been brought about entirely by the elimination of unfit mutations through natural selection.

Thus their case is entirely dependent on a demonstration that all trends observed in the evolution of all groups are adaptive, i.e., so useful to the organism that natural selection can take hold of them. It appears to me, as it has to others, that it is fairly easy to show that many of these trends are not so related.

I have alluded to a few instances of this but there is no time tonight to take up the evidence in detail.

So here I must rest my case.